

Phytoplankton Productivity

Carbon Assimilation in Marine and Freshwater Ecosystems

Edited by

Peter J. le B. Williams* David N. Thomas* and
Colin S. Reynolds**

*School of Ocean Sciences, University of Wales, Bangor, UK

**Centre for Ecology and Hydrology, Windermere, UK

Blackwell
Science

Chapter 7

Assessment of Primary Production at the Global Scale

Michael J. Behrenfeld, Wayne E. Esaias and Kevin R. Turpie

7.1 Introduction

Since the evolution of the first photosynthetic organisms some 3.8 billion years before present (Schopf, 1983), photoautotrophic organisms and the communities they support have continuously altered the chemical composition of the oceans and, through exchange across the air-sea interface, influenced the composition of the overlying atmosphere. Variations in the concentration of radiatively sensitive gases in the atmosphere (e.g. CO₂, CH₄), in turn, influence global climate and consequently ocean circulation, stratification, and the transport of dust to remote ocean regions. These physical forcings govern spatio-temporal variability in phytoplankton distributions through the direct effect of temperature on growth and through their secondary influence on factors such as mixed-layer light availability and the distribution of macro- and micro-nutrients. Perhaps beyond any other observations, satellite measurements of global phytoplankton pigment concentrations have most clearly demonstrated this dependence of ocean productivity on physical processes.

Biogeochemical cycles in the oceans are clearly not in steady state (Falkowski *et al.*, 1998). Biological responses to global perturbations in the physical environment are delayed by the buffering effects of ecosystem complexity. An urgency to characterise such physical-biological feedbacks developed during the final decades of the twentieth century due to escalating public and scientific concerns that environmental impacts of human activities were transitioning from the local to the global scale. At the forefront of these emergent global issues is the potential for a change in climate resulting from rising atmospheric concentrations of carbon dioxide and other 'greenhouse' gases. Unquestionably, sequestration of CO₂ by the photosynthetic biosphere (land and oceans) will play a critical role in future climate trends, but quantifying this CO₂ exchange and its temporal sign remains an uncertainty in global climate models (GCMs).

The most accurately constrained carbon fluxes in GCMs are the release from fossil fuel combustion (presently, $5.5 \pm 0.5 \times 10^{15}$ g C y⁻¹ = 5.5 petagrams (Pg) y⁻¹) and atmospheric CO₂ accumulation (3.3 ± 0.2 Pg C y⁻¹). Less well quantified is the

terrestrial carbon source from land-use change and deforestation, estimated at $1.6 \pm 1.0 \text{ Pg C y}^{-1}$ (Sarmiento and Wofsy, 1999). Thus, of the 7.1 Pg C released annually, 3.3 Pg C y^{-1} are retained in the atmosphere and the remaining 3.8 Pg C are removed both abiotically and through photosynthetic fixation. Based on ≈ 2 million measurements of the partial pressure of CO_2 over the oceans ($p\text{CO}_2$) collected across 25 years, the annual oceanic sink for CO_2 has been estimated at $2.0 \pm 0.8 \text{ Pg C}$ (Sarmiento and Wofsy, 1999). Balancing the global CO_2 budget thus requires an additional sink of $1.8 \pm 1.6 \text{ Pg C y}^{-1}$. This ‘missing sink’ is assumed to involve the biosphere and likely entails both oceanic and terrestrial components. Partitioning of the unaccounted carbon between the land and oceans is difficult, however, because it represents less than 2% of biospheric net primary production, estimated at $111\text{--}117 \text{ Pg C y}^{-1}$ (Behrenfeld *et al.* 2001a).

7.6 Summary

Primary productivity models, when coupled with time-varying global measurements of phytoplankton biomass, provide critical information for detecting changes in oceanic carbon fluxes. Such models are also beneficial for assessing ecological responses to regional changes in nutrient loading and may provide estimates of biologically mediated long-term carbon sinks if linked to secondary models of export production. The foundation of both aquatic and terrestrial NPP models is similar and, in the simplest terms, can be described as equating NPP to the product of plant biomass and light utilisation efficiency. From this basic relationship, a wide variety of phytoplankton productivity models have developed. At the categorical level, these models differ with respect to the presumed importance of resolving the time, depth, and spectral dependence of photosynthesis. Within each model category, differences largely centre around the specific treatment of the photosynthesis-irradiance relationship and in the characterisation of the underwater light field.

In this chapter, we have attempted to describe the relationship between various NPP models and the assumptions required to progress from fully expanded WRMs to the very simple DIMs. We have argued that all global estimates of NPP are critically dependent on the approach employed for modelling light-saturated photosynthesis and demonstrated this conclusion using two temperature-dependent models and a new light-nutrient model. This later model produces ΣNPP estimates comparable with local-scale, daily ^{14}C -uptake results. Although the model was applied to global satellite C_{sat} data using a simple DIM formulation, its description at the level of chlorophyll synthesis and Calvin cycle reactions is ideally suited for application in a WRM. The primary advantage of using a spectrally resolved model will be the improved estimates of mixed-layer acclimation irradiances, which are a primary forcing factor for variability in P^b_{max} .

Over the 50 year history of productivity modelling, significant advances have been made toward assessing global-scale phytoplankton photosynthesis. Noteworthy accomplishments include the development of variable P^b_{max} models; characterisation of the underwater light field; description of vertical variability in phytoplankton biomass distributions, and the development of remote sensing capabilities that now provide global measurements of near-surface chlorophyll every two days. These achievements notwithstanding, we hope our discussion has impressed upon the reader the need for further improvements in primary productivity modelling. These improvements will require laboratory, field, computational and remote sensing components, all of which represent exciting challenges for future research programmes.